

Effects of food abundance and habitat structure on seed-eating rodents in Spain wintering in man-made habitats

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Abstract

The patterns of abundance and seed (acorn) predation rates were analyzed in granivorous rodents (mainly the wood mouse *Apodemus sylvaticus* L.) wintering in two man-made habitats: cereal croplands, and a kind of wood-pasture exclusive to the western Mediterranean basin, the dehesas. Both seed (acorn) abundance and vegetation structure were also measured. Within dehesas, neither rodent abundance nor acorn predation rates were related to acorn abundance, whereas there was a significant association between rodent abundance and shrub cover at the end of winter. These results were coincident with previous findings in croplands. Both rodent abundances and seed predation rates were lower in dehesas than in croplands, despite the better structural and trophic conditions of the first habitat for rodents (larger shrub cover and food abundance). However, the body condition of animals was better in dehesas, to the extent that we found strong evidence for winter reproduction. Rodent predator communities appear to be more diverse and denser in dehesas than in croplands. This suggests a heavier predation pressure in dehesas which would have culled rodent populations in such a way that food was plentiful for survivors, thus explaining their scarcity, good body condition, and low dependence on food resources.

Introduction

Patterns of rodent abundance and seed predation rates have been intensively studied in the last few years, focussing mainly on deserts throughout the entire world (BROWN et al. 1975; MARES and ROSENZWEIG 1978; ABRAMSKY 1983; MORTON 1985). Experimental studies have shown that seed availability (PRICE and WASER 1985), shrub cover (BROWN 1988) and moonlight levels (KOTLER et al. 1991; LONGLAND and PRICE 1991) are the main factors influencing desert rodent abundance and seed predation patterns by their effect on food intake rates and predation risk (SIMONETTI 1989). In man-modified habitats such as cereal croplands, however, a recent study (DÍAZ 1992) showed that seed abundance was of minor importance to seed-eating rodents (mainly the wood mouse *Apodemus sylvaticus* L.). This seems to be caused by the strong demand by rodents for safe refuges and foraging sites during winter (DÍAZ 1992).

The aim of this study is to analyse the winter patterns of abundance and seed (acorn) predation rates of rodents inhabiting a kind of wood-pasture exclusive to the western Mediterranean basin, the dehesas (CAMPOS and MARTIN 1987). This man-modified habitat consists of cleared oak woodlands with open grasslands and Mediterranean scrub. Their management (tree clearing, cereal sowing, and shrub removal by ploughing) produces a mosaic of plots that differ in soil and understory vegetation characteristics (stability, herb and shrub cover) in a similar way to croplands (DÍAZ 1992), so that we can compare the results obtained with the findings outlined above.

Material and methods

Study area

Data were collected in the Tiétar valley, 15 km SW of Candeleda (40° 06' N, 05° 17' W, about 300 m a.s.l.), central Spain. The climate is humid Mediterranean with hot summers and mild winters (MINISTERIO DE AGRICULTURA 1981). The study area is covered mainly by holm oak *Quercus ilex* L. dehesas, with some interspersed cork oak *Q. suber* L. and ash *Fraxinus excelsior* L. trees growing along seasonal streams. The main shrub species are *Crataegus monogyna* Jacq., *Lavandula stoechas* L., *Halimium ocymoides* (Lam.) Willk., *H. viscosum* Willk., and saplings of the dominant tree species. The herb layer is composed mainly of *Trifolium* spp., *Ornithopus compressus* L., *Vulpia* spp., *Poa bulbosa* L., *Tuberaria guttata* (L.) Fourc., and *Leontodon* spp. Small plots sowed with cereals (mainly oats *Avena sativa* L. and rye *Secale cereale* L.) are also present.

Sampling design

Twelve 500 × 100 m plots were established in the study area. Four of them were ploughed and sowed with oats and rye in September 1990, four had been intensively grazed by sheep and cattle during the last ten years, and four had not been ploughed in the last twenty years and were only lightly grazed by cattle. The plots were selected to represent these three management types of dehesas (hereafter called cultivated, grazed, and shrubby dehesas, respectively; see CAMPOS and MARTIN 1987), and they were located forming pairs or trios in contact zones between management types whenever possible.

On each plot, we marked twenty holm oak trees in October 1990, under whose canopies we carried out acorn censuses and measured rodent acorn predation rates. Holm oaks were selected by walking a 500 m transect along the middle of the plot, and marking the nearest tree at either side of the progression line at 25 m-intervals. In March 1991 we selected twenty additional trees in each plot for rodent trapping. Each of them was located between each pair of consecutive trees previously chosen, plus one more located at approximately 15 m from the last marked tree.

Acorn abundance

We established two 0.5 × 0.5 m permanent squares under the canopy of each of the 240 trees marked in October 1990. The positions of the squares were chosen at random following the procedure proposed by SKALSKI (1987). The diagonal of each square was marked by means of two nails pinned in the ground. We counted the holm oak acorns present within a square iron frame placed between each pair of nails. Acorn censuses started with one count made in late October 1990, and then continued at two week intervals from late November 1990 to mid March 1991.

Rodent predation rates

The impact of rodents on acorns was assessed in December 1990, January 1991, and February 1991. The acorns present in the permanent squares were counted at dusk and at dawn of one sampling night per month, corresponding to the dark moon phase to eliminate the effect of moonlight on rodent foraging activity (KOTLER et al. 1991; LONGLAND and PRICE 1991). The difference between these two counts was assumed to be the number of acorns taken by rodents during one night, since no other nocturnal acorn predators (red deer *Cervus elaphus* L., wild boar *Sus scrofa* L.) were noticed in the study plots. Results of the dusk censuses were also used as an estimate of the acorn abundance at these dates. Acorn predation rates were not measured in October and November because acorns were still falling from the trees at these dates.

Vegetation structure

Vegetation structure of each study plot was quantified by use of 100 scored sticks that were placed vertically on the ground at 5 m intervals over a line transect. We used the stick to assess whether vegetation was contacted at 10 cm-height intervals from the ground level to 1 m height or more; if positive, the life form (herb or shrub) of the plant(s) contacted was noted. We also considered the presence or absence of leaf litter, stones or bare ground at the 0 cm level (see e.g. DÍAZ and CARRASCAL 1991). This technique provided detailed descriptions of the structure of the vegetation based on objective percentage covers (number of positive contacts out of the 100 sample points). The height of the understory vegetation was also measured at each sample point by noting the highest plant contact with the stick to the nearest 5 cm. All these measurements were taken in November–December 1991, just before winter freezing temperatures interrupt vegetation growth until next spring (PEREZ 1988). Tree cover was estimated by counting the number of trees on aerial photographs of

the study plots, and then computing their cover by assuming a mean canopy radius of 6 m ($N = 76$ trees; $SE = 0.2$ m). We then performed a Principal Component Analysis (see THOMPSON et al. 1991 for a similar approach) on these data to reduce the number of structural variables with a minimum loss of information. Since we only took twelve measures, we had to reduce the set of variables before analysis. This was done by pooling the covers of bare ground, litter and stones in an "unvegetated ground cover" variable, and by considering the herb and shrub covers in only three height intervals (0, 0–50, and > 50 cm height).

Rodent abundance

Rodent abundance in each plot was estimated in March 1991. Two snap-traps were placed close to the trunk of each of the forty holm oak trees per plot previously selected. Trapping started on 9th March and lasted three consecutive dark moonlit nights. All the rodents caught were identified to the species level, weighed, and dissected to determine sex, reproductive state (testes enlarged or not in males, and lactancy or pregnancy in females), and body size (measured as condylo-basal length of the skull; ALCANTARA and DÍAZ 1993).

Results

Vegetation structure

Cultivated plots were characterized by their large covers of bare ground, and of herbaceous plants at 0–50 cm height. Grazed plots showed large herb covers at the ground level, but these covers decreased sharply as height increased, thus giving the shortest mean vegetation heights. Finally, shrubby plots showed the tallest mean vegetation heights, as well as large shrub covers between 0 and 50 cm in height (Tab. 1). The first principal component

Table 1. Average ($\pm SE$) values of vegetation structure variables according to the management type of study plots, and correlation coefficients between those variables and the two first factors obtained in the Principal Component Analysis of vegetation structure

Variable	cultivated	grazed	shrubby	PC I	PC II
Total cover of herbs (%)	84.0 \pm 8.7	76.8 \pm 13.0	73.5 \pm 4.9	0.418	0.182
Total cover of shrubs (%)	0.0 \pm 0.0	1.0 \pm 0.8	36.0 \pm 14.3	-0.988**	0.041
Cover of trees (%)	23.6 \pm 9.3	23.8 \pm 9.4	22.7 \pm 10.5	-0.152	-0.108
Cover of unvegetated ground (%)	54.0 \pm 16.2	25.0 \pm 11.5	32.3 \pm 3.9	0.323	0.842**
Cover of herbs at > 50 cm height (%)	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.5	-0.659**	0.094
Cover of herbs at 0–50 cm height (%)	23.0 \pm 16.4	6.5 \pm 3.3	15.8 \pm 6.7	0.269	0.822**
Cover of herbs at 0 cm height (%)	83.8 \pm 8.3	76.0 \pm 12.6	70.8 \pm 3.9	-0.245	-0.866**
Cover of shrubs at > 50 cm height (%)	0.0 \pm 0.0	0.0 \pm 0.0	11.0 \pm 6.7	-0.933**	0.169
Cover of shrubs at 0–50 cm height (%)	0.0 \pm 0.0	0.5 \pm 0.6	25.5 \pm 10.5	-0.981**	0.033
Cover of shrubs at 0 cm height (%)	0.0 \pm 0.0	0.8 \pm 1.0	17.5 \pm 4.7	-0.823**	0.099
Mean vegetation height (cm)	12.9 \pm 3.3	4.7 \pm 1.5	38.3 \pm 17.3	-0.733**	0.581
Eigenvalue				4.89	2.57
% variance				44.5	23.3
Σ % variance					67.8

* = $p < 0.05$; ** = $p < 0.01$. $df = 10$.

obtained in the analysis of these variables is an inverse gradient of shrub cover and vegetation height, and it segregates the shrubby plots from those grazed or cultivated (Tab. 1, Fig. 1). The second component segregates the plots according to the structure of their herb layer. It correlates positively with herb cover at 0–50 cm and with the cover of unvegetated ground, and negatively with herb cover at the 0 cm level; hence it segregates cultivated plots from grazed ones (Fig. 1).

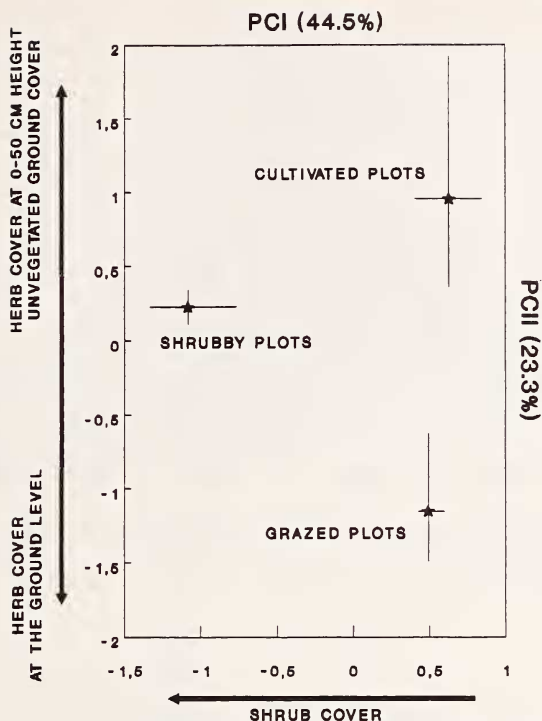


Fig. 1. Mean coordinates of the three management types of plots ($N=4$ for each management type; lines show ranges) in the plane defined by principal components I and II of the analysis of vegetation structure. Both percent variances explained and the interpretation of each component are also shown

Acorn abundance

Mean acorn abundances ranged between 26.08 per m^2 in cultivated plots in December and 0.75 acorns m^{-2} in grazed plots in March. A three-way ANOVA analysis on log-transformed numbers of acorns per square (average values of the two squares under each tree) showed highly significant effects ($p < 0.001$) of both plot, type of management and sampling date. There were also significant plot-habitat and date-habitat interactions. The plot-date interaction, as well as the three-way interaction term, were not significant, i.e. the mean acorn abundances showed changing patterns of spatial and temporal variability, whereas the trends showed by each plot were constant over time. Cultivated plots had on average larger acorn abundances than grazed and shrubby ones at any sampling date, except at the late October census. Peak acorn abundances were not synchronized in the three management types; they were reached in late November in shrubby plots, in mid December in grazed ones, and in late December in cultivated ones (Fig. 2).

Rodent abundance and acorn predation rates

We captured 30 rodents (18 wood mice *Apodemus sylvaticus* L., 2 Algerian mice *Mus spretus* Lataste, and 10 garden dormice *Eliomys quercinus* L.) in 2880 trap-nights (240 trap-nights per plot; Fig. 3). Overall trapping success differed between species only when the analysis was carried out over the whole data base (fit of log-linear models to the four-way contingency table generated by the factors plot \times management type \times species \times presence/

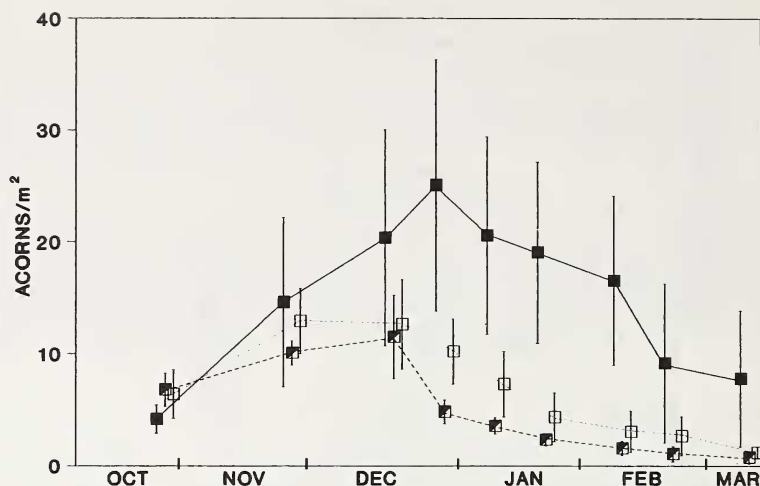


Fig. 2. Mean (\pm SE) numbers of acorns m^{-2} according to sampling date and the management type on plots (filled squares: cultivated; half-filled squares: grazed; empty squares: shrubby). $N=4$ by each management type, except for cultivated and grazed in late December, when only three plots of each could be censused

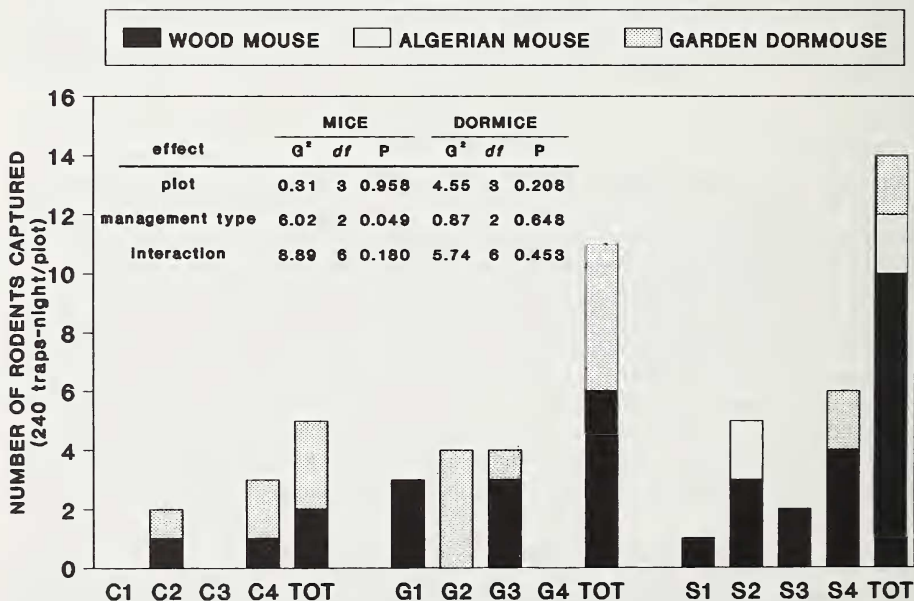


Fig. 3. Rodent captures of each species in each study plot (C1-4: cultivated; G1-4: grazed; S1-4: shrubby). Results of the fit of log-linear models (SOKAL and ROHLF 1981; HEISEY 1985) for the three-way contingency tables generated by the factors plot \times management type \times presence/absence of capture are also shown for each rodent species (both mice grouped for analysis)

absence of capture [SOKAL and ROHLF 1981; HEISEY 1985]; $G^2 = 8.42$, $P = 0.015$, $df = 2$ for the species effect; $P > 0.2$ for the effects of the remaining factors and factor interactions). However, when the analyses were carried out separately for each rodent species (both mice species pooled because of their quite similar foraging behaviour; see DÍAZ 1992), a significant effect of plot management on mice abundance was detected. Mice were most abundant in shrubby plots and least abundant in cultivated ones, whereas dormice abundance was not affected by this factor (Fig. 3). This latter species hibernates from November to March in central Spain (PALACIOS 1974), so it is unlikely that the animals captured were active when acorn predation rates were measured. Moreover, this species is mainly arboreal, so that it is unlikely that the soil and understory modifications considered here would affect its populations. Thus, we will not further consider the garden dormice.

The number of acorns taken by rodents per square meter decreased significantly from the beginning of winter onwards (Fig. 4), the spatial pattern of this variable being, however, statistically indistinguishable from evenness (three-way ANOVA on the average number of acorns taken from the two quadrats located under each marked tree, log-transformed; $F_{2,674} = 7.25$, $P < 0.001$ for the effect of sampling date, $p > 0.05$ for the effects of plot, plot management, and all factor interactions).

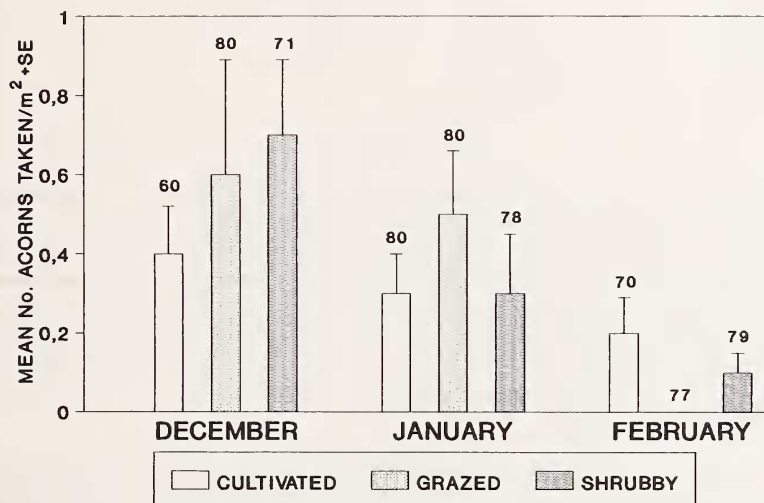


Fig. 4. Average acorn predation rates according to sampling date and the management type of plots. The figures over the bars indicate the number of oak trees sampled

Mice abundance was significantly correlated with shrub cover (inverse of PCI; $r = -0.62$, $P < 0.05$, $N = 12$ plots), but not with acorn abundance or with the characteristics of the herb layer (PCII). The correlation coefficients between mice abundance and rodent predation rates were not significant. Rodent predation rates were not correlated with any structural gradient or with acorn abundance at any sampling date.

Comparisons with cereal croplands

Results obtained show (Tab. 2) that both mice abundance and rodent seed predation rates were larger in croplands than in dehesas (about 4.5 and 6 times larger, respectively). Both average shrub cover and food abundance were, however, much larger in dehesas than in croplands (12 times larger for cover, and about one order of magnitude larger for food abundance, even without considering any other seed but acorns in dehesas). The average

Table 2. Comparisons of average mice abundances, rodent seed predation rates, body mass, body size, and body condition of mice populations wintering in cereal croplands (from DÍAZ 1992) and in dehesas

Average food abundance and shrub cover of both habitat types are also shown. See Appendix for the methods used to reduce these variables to common, comparable units

	Dehesas	Croplands	
Rodent abundance (rod./100 trap-nights)	0.69 (N = 2880)	3.14 (N = 1052)	$G_1 = 29.9^{***}$
Seed predation rates (% seeds preyed upon)	2.91 (N = 1222)	18.60 (N = 264)	$G_1 = 68.1^{***}$
Body mass (g; $\bar{X} \pm SE$)	26.3 ± 2.5 (N = 12)	18.2 ± 0.5 (N = 26)	$F_{1,36} = 20.1^{***}$
Body size (CBL) (mm; $\bar{X} \pm SE$)	23.6 ± 0.3 (N = 12)	23.1 ± 0.2 (N = 26)	$F_{1,36} = 1.9^{n.s.}$
Body condition ($\bar{X} \pm SE$)	2.0 ± 1.4 (N = 12)	-0.1 ± 0.1 (N = 26)	$F_{1,36} = 5.2^*$
Food abundance (kJ seeds/ha)	1.6×10^6	2.6×10^5	
Shrub cover (%) ($\bar{X} \pm SE$)	12.4 ± 5.5 (N = 12 plots)	0.1 ± 0.1 (N = 264)	$t_{274} = 12.1^{***}$
*** = $p < 0.001$; * = $p < 0.05$; n.s. = $p > 0.05$.			

body mass of wood mice wintering in dehesas was larger than that of mice inhabiting croplands (Tab. 2); their body size, however, did not differ between these two habitats, whereas the body condition of mice was better in dehesas than in croplands (Tab. 2). Moreover, we found strong evidence for winter breeding in dehesas: 8 out of 10 male wood mice showed enlarged testes in early March and, out of 7 females, 3 were lactating, one was pregnant, and two were probably less than 9 weeks old (they both weighed less than 20 g and showed a dark grey fur; CORBET and SOUTHERN 1977; GURNELL and KNEE 1984). In croplands, only 2 out of 20 males captured showed enlarged testes, and none of the 11 females were lactating or pregnant.

Discussion

Concerning their carrying capacity, dehesas seem to be a poor wintering habitat for rodents, since they support very low population densities as compared with croplands. This situation cannot be attributed to worse trophic conditions because, on the one hand, food abundance in dehesas seems to be quite large, and on the other hand, the body condition of mice inhabiting dehesas was much better than those of mice inhabiting croplands, to the extent that they could have bred during winter (winter sexual activity in rodents is mainly related to adequacy of food conditions; CLARKE 1985; HANSSON 1984). Moreover, neither rodent abundance nor rodent predation rates were associated to food abundance within dehesas at any date, and rodent foraging impact appeared to be too low to deplete food resources significantly.

Two other factors apart from food abundance have been postulated as being primary in regulating rodent abundance: the availability of home sites, and the effectiveness of agents affecting life-spans (PENNYCUK et al. 1987). The main process affecting life-spans in small rodents seems to be predation pressure, that in turn is related to predator abundance (e.g. STEEN et al. 1990) and to the availability of safe foraging places such as shrub understories. From this point of view, dehesas would have been more populated than croplands, since

they offer stable ground everywhere to build refuges (the area close to the tree trunks is never ploughed), and their average shrub cover was also larger. Contrary to these expectations, dehesas seem to maintain lower rodent population densities than croplands. Dehesas are inhabited by a diversified, and probably dense, rodent predator community (four owl species – *Tyto alba* Scopoli, *Athene noctua* Scopoli, *Strix aluco* L., and *Asio otus* L. – and four carnivore species – *Vulpes vulpes* L., *Mustela nivalis* L., *M. putorius* L., and *Genetta genetta* L.), whereas in croplands most rodent predators have been excluded by human activities (only *T. alba*, *A. noctua*, *V. vulpes*, and *M. nivalis* were present). These data, although rather qualitative, suggest that rodents in dehesas would have been subjected to a heavier predation pressure than in croplands.

Following this argument, close associations to shrubby plots within dehesas should have been found if predation risk would have been consistently important all through the winter (BROWN 1988; SIMONETTI 1989; DÍAZ 1992). This association, however, was only evident at the end of winter, whereas acorn predation rates did not show any pattern of association with vegetation structure. This result could have arisen from the fact that acorn predation rates were measured in dark moon nights only. There is both direct and indirect evidence that low levels of nocturnal illumination relax predation risk, thus permitting wide movements of rodents from daylight refuges (KOTLER et al. 1991; LONGLAND and PRICE 1991; DÍAZ 1992). These refuges could be built up even in the most heavily managed plots since the area close to the tree trunks remains unploughed. Predation pressure, however, would have culled rodent populations faster in cultivated and grazed plots, where foraging animals would have been more exposed to predators because of the scarcity or lack of protective cover, than in shrubby ones.

Summarizing, rodent populations in dehesas appeared to be maintained at low levels by the combined effect of a heavy predation pressure and a man-made scarcity of safe foraging places. This culled situation could have been the cause of the low importance of food resources in determining intra-dehesas patterns of rodent abundance and acorn predation rates. Furthermore, the large abundance of food resources in relation to the demands of a culled population might have produced an excess of food for survivors during the winter, which could explain their good physiological condition (PENNYCUK et al. 1987; DESY and BATZLI 1989).

Appendix

Methods used to reduce the variables considered in table 2 to common units

Seed predation rates: computed as the percentage of seed trays visited over the number available in croplands (DÍAZ 1992), and as the average percentage of acorns predated over the number available in each of the three sampling periods (December, January, and February) considered in this study.

Body condition of wood mice: residuals from the regression model relating body weight (\bar{W}) and condylo-basal length (CBL): $W = 0.0005 \text{ CBL}^{3.41}$; $R^2 = 44\%$; $p < 0.01$; $N = 163$ wood mice wintering in a wide array of habitat types from central Spain (ALCANTARA and DÍAZ 1993).

Energy value of seeds: according to DÍAZ (1991) for croplands. For dehesas, this value was computed from the mean density of acorns in midwinter months – January and February; see figure 2 –, the average dry weight of acorns in the study area –1.48 g; $N = 4941$ – the mean nutrient composition of holm oak acorns – see HERRERA (1977) –, and the caloric values of proteins, fats, and carbohydrates given by GLÜCK (1985).

Shrub cover in croplands: measured on 1-m² sampling plots around each seed tray (see DÍAZ 1992). Data arcsin-transformed before analysis.

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Zusammenfassung

Auswirkungen von Nahrungsüberfluß und Habitatstruktur auf Körner fressende Rodentia, die in Spanien in von Menschen geschaffenen Lebensräumen überwintern

Die Studie analysiert die Auswirkungen von Überfluß an Getreidekörnern und Eicheln auf Körner fressende Nagetiere, die in von Menschen geschaffenen Habitaten überwintern (hauptsächlich Feldmäuse, *Apodemus sylvaticus* L.). Es geht um zwei verschiedene Lebensräume: Getreidefelder und lichte Steineichenwälder im Westen Spaniens, dehesas genannt. In den dehesas wurde kein Zusammenhang zwischen den großen Mengen an Eicheln und einer möglichen Überpopulation an Nagern festgestellt. Die große Nagerpopulation im Winter ist eindeutig auf den dichten Buschbestand zurückzuführen. Dieses Ergebnis stimmt mit vorherigen Studien überein. Obwohl die dehesas den Nagern bessere Lebens- und Nahrungsbedingungen bieten, ist die Anzahl der Nager geringer als in den Getreidefeldern. Die Nager der dehesas sind jedoch in einem besseren körperlichen Zustand als ihre Artgenossen in den Getreidefeldern; sie vermehren sich sogar im Winter. Außerdem scheinen die Nagerpopulationen der dehesas dichter und vielseitiger zu sein. Die relativ geringe Anzahl an Nagern trotz besserer Lebensbedingungen ist nur dadurch zu erklären, daß die Populationen durch den erhöhten Druck von Raubtieren dezimiert werden. Den überlebenden Nagern steht so ein reichhaltiges Nahrungsangebot zur Verfügung, Grund für ihre gute körperliche Verfassung und ihre weitgehende Unabhängigkeit von speziellen Nahrungsquellen.

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